13. An Experimental Determination of the Factors which cause Patterns to appear Conspicuous in Nature. By J. C. Mottram, M.B. (Lond.)*.

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(Text-figures 1–20.)

Index.

Introduction.

It is an undisputed fact that patterns often render animals inconspicuous in Nature. These patterns have definite characters on which their inconspicuousness depends, and in a previous paper (P. Z. S. 1915, p. 679) some of these characters were defined. Just as against any single background, or against any series of backgrounds, patterns can be placed which will appear inconspicuous, so other patterns can be placed which will appear relatively conspicuous. Experiments were carried out to determine the characters which render patterns conspicuous, and these are dealt with in Part I. of this paper. Having defined the factors for conspicuousness, the Indian Diurnal Lepidoptera were examined to see whether any of these insects presented patterns which must render them conspicuous. Part II. deals with this consideration.

Part I.

Scheme of Description.

Experiments were carried out with artificial patterns, against artificial backgrounds. These are described under four headings;—

(A) The consideration of plain objects against plain backgrounds.
(B) The consideration of patterned objects against plain backgrounds.
(C) The consideration of plain objects against patterned backgrounds.
(D) The consideration of patterned objects against patterned backgrounds.

The experimental conditions are shown in text-fig. 1; standard

* Communicated by the Secretary.

candles were used. In order to obtain a series of backgrounds ranging from dark to light tone, the object was fixed on a glass plate and was illumined separately from the background, as shown in text-fig. 1, B; by moving the background near to or away from its illumination, and by using backgrounds of different tones, it was possible to obtain every grade of tone, from black to white.

In these experiments tone is alone considered; colour was kept constant by using only black, white, and neutral greys.

(A) *Plain Objects against Plain Backgrounds.*

Plain objects may enter into consideration of pattern, because they are in reality objects covered by a very small pattern. The visibility of plain objects was found to be affected by the following factors:—the human eye, the lighting, the atmosphere, the background, and the object.

The human eye, even when it does not present some gross defect, nevertheless is found to vary from individual to individual; so that the readings made by one person cannot be directly compared with those of others. Working with the same eye, several factors affect visibility; if the eye be allowed to become fatigued, the greatest distance at which objects can be seen is much reduced. Experiments showed that from thirty to forty observations could be made during two hours without encountering fatigue effects.

Some time must be allowed for the eye to become accommodated to a sudden change in illumination: for a change from daylight to almost complete darkness, twenty minutes is necessary; working with two standard candles, it was found that fifteen minutes must be allowed.

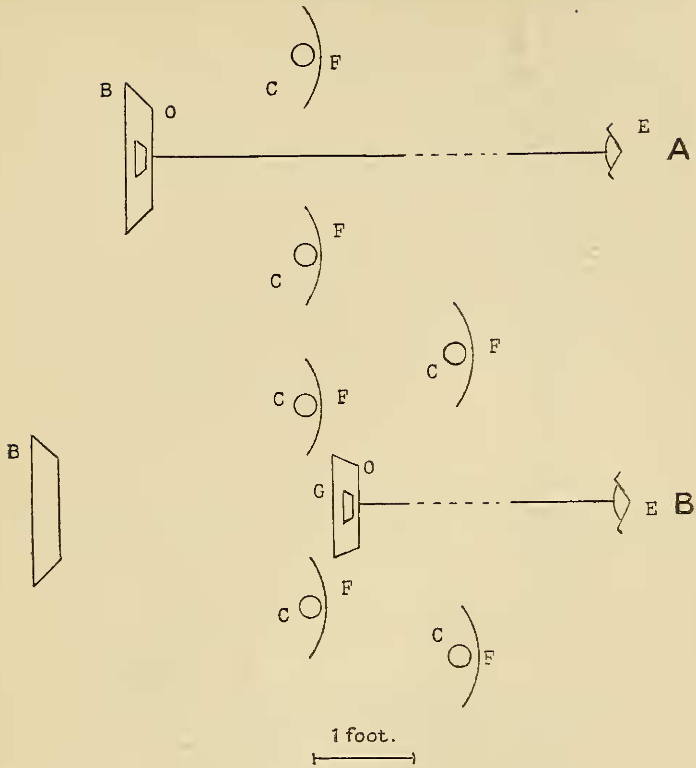
The eye was also found to vary somewhat from day to day: health and general fatigue are probably the cause of these variations. Owing to this, one cannot directly compare the reading of one day with that of another. The accuracy with which measurement can be made is indicated in experiment no. 1.

The effect of the opacity of the air on visibility does not enter into these experiments, as no measurements beyond eighty feet were made, and observations were not made during fogs.

The Effect of Lighting.—Experiments showed that the greater the illumination the greater the distance at which objects can be seen, all other factors remaining constant.

The Effect of the Background.—A plain object is visible at a great or small distance according as to whether the difference in the amount of light coming from the object and the background is great or small. A white object is more visible against a black background than against a grey one, and more visible against a dark-grey than against a light-grey one. Experiments were not carried out to define this relation more accurately; but the

Text-figure 1.



Ground plan of apparatus used for measuring visibility of objects and blending distance of patterns. A = when object and background are illuminated by the same light. B = when illuminated by different light.

C=standard candles, F=screens, E=eye, B=background, O=object, G=glass plate.

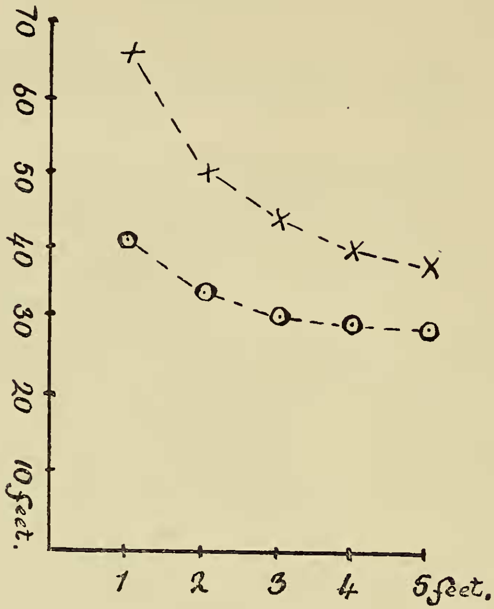
EXPERIMENT No. 1.

A. Candles 1 ft. apart: conditions as in text-fig. 1: candles distant 1 ft. from glass plate on which object was placed: background of grey paper 2 ft. from glass plate. Object of black needle-paper, 36 sq. mm. The following ten readings (in feet) of the greatest distance at which the object could be seen, were made at intervals of five minutes:—72, 72·8, 72·9, 72·8, 74·4, 73·4, 74·1, 73·5, 72·7, 72·9.

B. Candles 1 ft. apart: patterns 2 ft. 1 in. from candles: pattern consists of alternate black and white squares, 25 sq. mm.: pattern covered, 16 sq. cm. The following ten readings (in feet) of the distance at which the pattern blended into an even grey tone, were made at intervals of five minutes:— 31, 33, 33·6, 34·1, 34, 33·9, 34·5, 33·7, 33·8, 34·3, 34.

following experiment (no. 2) was made as it has a bearing on the relative visibility of patterns, as will appear later. It shows that a constant-in-tone contrast between object and background does not result in a constant visibility.

Text-figure 2.



Relative visibility of objects.

Ordinates = distance at which object is visible.
Abscissæ = distance of candles from object.

X = white object against black background.
⊙ = black object against white background.

Experiment No. 2.

Experimental conditions as in text-fig. 1. Candles 1 ft. apart.

Materials:—Backgrounds: white, of white Bristol board 100 sq. cm.; black, of black needle-paper 100 sq. cm. Objects:—White, of white Bristol board 4·5 sq. cm.; black, of black needle-paper 4·5 sq. cm.

Results (mean of three observations).

When distance from candles to object was	white square was visible against black background at	black square was visible against white background at
1 foot	66·5 feet	41·6 feet
2 feet	50·4 ,,	34·4 ,,
3 ,,	44·1 ,,	32·2 ,,
4 ,,	40·9 ,,	31 ,,
5 ,,	37·2 ,,	30·7 ,,

This experiment shows that a white object on a black background is more visible than a black object on a white ground. It can be seen (text-fig. 2) that the higher the illumination the greater the difference; at low illuminations the curves of visibility approach one another (they would meet at complete darkness). The same was found to be the case when object and background were of different shades of grey, instead of black and white. The light-grey object against the dark-grey background is more visible than the dark-grey object against the light background.

It was thought that the lower visibility of the black object on the white ground might be due to the dazzling effect of the large area of white. It was found that reduction in the area of the white background by means of black diaphragms produced the opposite effect, and, further, that the nearer the diaphragm was brought to the object the less visible the object became. It was further found that when the white square on the black background was similarly surrounded by white diaphragms, the same effect resulted (see experiment no. 3).

Experiment No. 3.

Experimental conditions as in text-fig. 1. Candles 1 ft. 6 ins. apart; distance of candles from object, 2 ft.

Materials:—Backgrounds of white Bristol board and black needle-paper, 100 sq. cm. Objects of same materials, 4·5 sq. cm. Black and white square diaphragms, total size 100 sq. cm., with a central square hole:

No. 1.	Size of central hole	was	64	sq. cm.
„ 2.	„	„	36	„
„ 3.	„	„	16	„
„ 4.	„	„	4	„
„ 5.	„	„	1	„
„ 6.	„	„	0·16	„

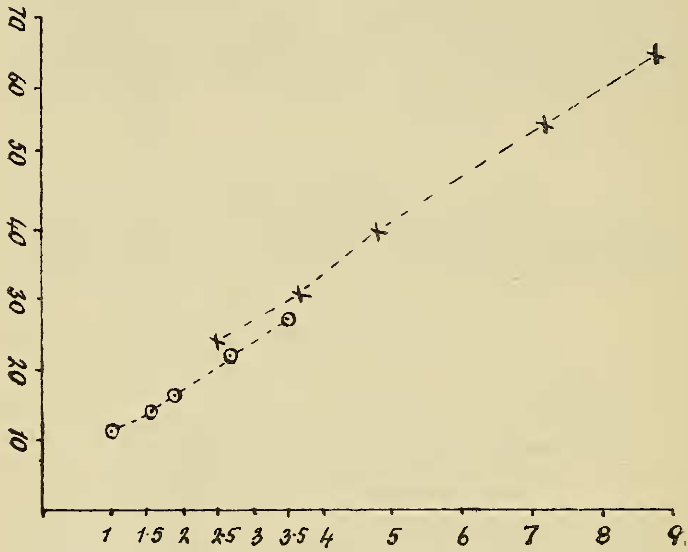
White object on black background was visible at					45·5	feet.
When surmounted by No. 1 white diaphragm, at					40·7	„
„	„	2	„	„	37·6	„
„	„	3	„	„	34·8	„
„	„	4	„	„	29·5	„
„	„	5	„	„	24·0	„
„	„	6	„	„	13·4	„
Black object on white background was visible at					38·4	feet.
When surmounted by No. 1 black diaphragm, at					32·2	„
„	„	2	„	„	30·5	„
„	„	3	„	„	30	„
„	„	4	„	„	29·6	„
„	„	5	„	„	21·7	„
„	„	6	„	„	15·5	„

(Above readings are the mean of three observations.)

It would thus appear that light tone on dark is more visible than dark on light. This has been considered to be due to the eye recognising the object, in one case by a positive image, in the other by the absence of stimulation. This fact is of considerable importance in regard to the visibility of animals in Nature: those exhibiting large areas of light tone must be considered to be, other things being equal, much more conspicuous than those which do not. For instance, a light-coloured butterfly flying across a meadow, or down a hedgerow, is visible at a much greater distance than a dark one.

This greater visibility of light-toned objects in Nature can easily be demonstrated by comparing the visibility of black and white discs against a great number of natural backgrounds: only against snow and certain parts of the sky is the white the less visible; against the vast majority of backgrounds the white is very much more visible.

Text-figure 3.



Visibility of objects in proportion to size.

Ordinates = distance (in feet) at which object is visible.
Abscissæ = size of object, in square millimetres.

Experiment No. 4.

Experimental conditions as in text-fig. 1. Candles 1 ft. apart and 2 ft. from object.

Materials:—Black and white backgrounds of Bristol board and black needle-paper. Objects:—Black needle-paper of the following sizes: 2·5, 3·7, 4·8, 7·2, and 8·8 sq. mm.; and white paper of the following sizes: 1, 1·6, 1·9, 2·8, and 3·5 sq. mm.

The above diagram shows the distance at which the black objects were visible against the white background (X) and at which the white objects were visible against the black background (⊙).

An even more convincing way of demonstrating this fact is to take a series of artificial backgrounds, from white, through grey, to black: find the background against which black and white are equally visible under some natural condition of lighting—for instance, in a wood; now compare this background with

Text-figure 4.

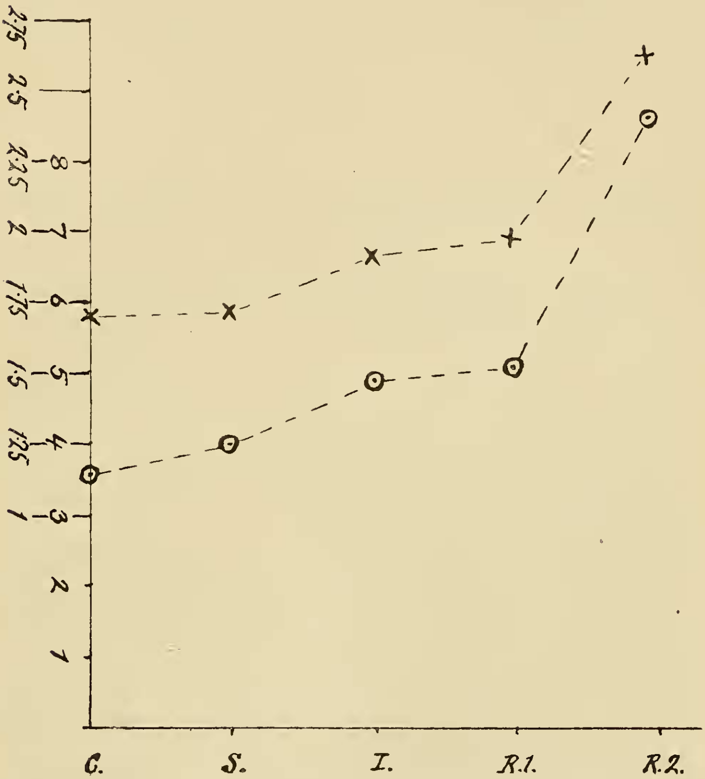


Diagram showing the correspondence between the visibility of objects of different shapes (circle, square, isosceles triangle, and rectangles) and the concentration of their areas.

EXPERIMENT No. 5.

Candles 1 ft. apart; objects distant from candles 1 ft. 6 ins.
Objects of black needle-paper, area 16 sq. mm.; background of white Bristol board.

Objects.	Distance at which visible, in feet.	Inverse figures.
Circle	59	170
Square	58	173
Isosceles triangle of 90° ...	53	190
Rectangle, 8×2...............	51	198
Rectangle, 16×1	38	263

(Mean of five readings to nearest whole number.)

	$\frac{\text{Circumference}}{\text{Area}}$
Circle	$\frac{2\sqrt{\pi x}}{x^2} = \frac{3{\cdot}56}{x}$.
Square	$\frac{4x}{x^2} = \frac{4}{x}$.
Isosceles triangle of 90°......	$\frac{(2+2\sqrt{2})x}{x^2} = \frac{4{\cdot}83}{x}$.
Rectangle, $2\times\frac{1}{2}$	$\frac{5x}{x^2} = \frac{5}{x}$.
Rectangle, $4\times\frac{1}{4}$	$\frac{8{\cdot}5x}{x^2} = \frac{8{\cdot}5}{x}$.

In text-fig. 4 the inverse visibility figures (X) are conventionally plotted with the numerator of the periphery over area (⊙). It can be seen that the visibility curve closely follows the concentration of area curve.

the surrounding natural backgrounds: it will be found that it is very much lighter in tone than the lightest natural background which can be found in the wood.

On referring to the diagram (text-fig. 2, p. 386) it can be seen that the difference in visibility between white and black is greater at high illumination than at low. It follows that at night white is, in Nature, not nearly so conspicuous with regard to black as it is during daylight.

Diurnal animals presenting a large area of white or light tone must therefore be considered to be much more conspicuous than nocturnal animals similarly patterned.

The Effect of the Object's Characters on Visibility.—The characters, size, and shape will affect the visibility of an object when all other factors are kept constant. When the contrast in tone between object and background is great (the object being light in tone and the background dark), the human eye is able to define an object subtending an angle of approximately one minute. Distinction must be made between the ability to define or focus, and that to see: the eye cannot define a star, although it may be able to see it.

Keeping the shape of the object constant, experiments show that visibility is directly proportional to size: the larger the object, the greater the distance at which it is visible.

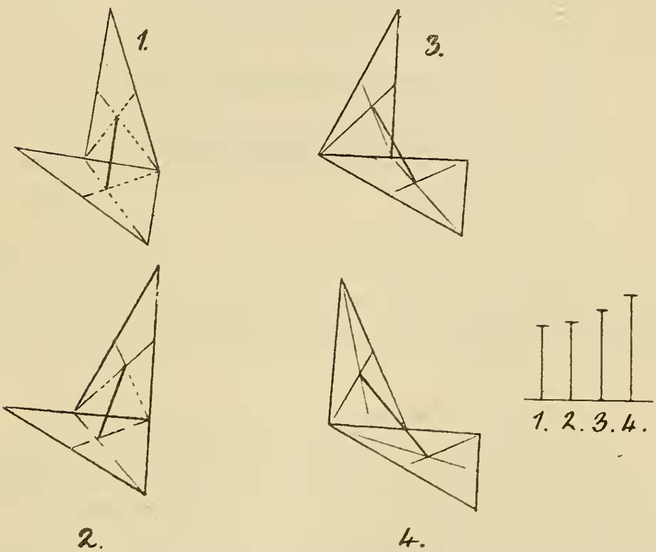
Whether the relation between size and visibility is the same for all shapes has not been determined; though during the course of this and other investigations a large number of shapes have been examined, no exceptions have been noted.

The visibility of objects is dependent upon their shape. Circles, squares, triangles, and rectangles of the same area are not equally visible. Experiments show that the more concentrated the area the greater the visibility.

In the following experiments concentration is measured by the ratio of circumference over area, and it can be seen that the distance at which the object is visible is inversely proportionate to this ratio (see experiment no. 5).

As a circle is the most concentrated form that an object can have, therefore it is the most visible form. The ratio circumference over area only gives the concentration for simple figures. Objects can be made of the same area and of the same circumference but of different concentration. In these cases concentration must be represented by the moment of area round the centre of area.

Text-figure 5.



Four figures of the same area and of the same circumference but which are not equally visible. The concentration of their areas is estimated by the length of the cord joining the centre of area of the two triangles.

Experiment No. 6.

Candles 1 ft. apart. Objects distant from candles 2 ft. 1 in.

Objects of black needle-paper, of the same area and having the same circumference, composed of two triangles as shown in the figure; the longest side measured 1·1 cm., the shortest ·5 cm., and the angle opposite the longest side was a right angle. Background of white paper.

Object.	Distance at which visible.
No. 1	51 feet.
„ 2	50 „
„ 3	47 „
„ 4	45·5 „

(Mean of six observations.)

The figure shows the lengths of the cords joining the centres of areas of the two triangles; it can be seen that when the cord is short and the area therefore concentrated, then the visibility is great, and *vice versa*.

In experiment no. 6 mathematical expressions are avoided by presenting the concentration as the length of a cord. Areas of the same size and circumference, but of different concentration, are dealt with in this experiment; and the same conclusion is arrived at, namely, that the more concentrated the area of the object the greater its visibility.

This completes the consideration of plain objects against plain backgrounds. The following facts have been observed :—

1. The greater the difference in the amount of light coming from an object and background, the greater the distance at which the object is visible.
2. A constant contrast in tone between object and background does not ensure a constant visibility. Dark objects against light backgrounds are less visible than light objects against dark backgrounds. This difference is greater at high illuminations than at low ones.
3. The larger the size of the object, and the greater the concentration of its area, the greater the distance at which it is visible.

It follows that a plain object will appear conspicuous against a plain background when the contrast in tone between object and background is great, and when the object is lighter rather than darker in tone than the background, and when its size is great and area concentrated.

(B) *Patterned Objects against a Plain Background.*

As long as the pattern of an object against a plain background is visible, the object must be visible. It follows that visibility will to some extent depend upon the blending distance of the pattern.

The following factors were found to affect the blending distance of patterns: lighting, contrast in tone between the components of the pattern, size of the components and shape of the components, and the relative size of the components.

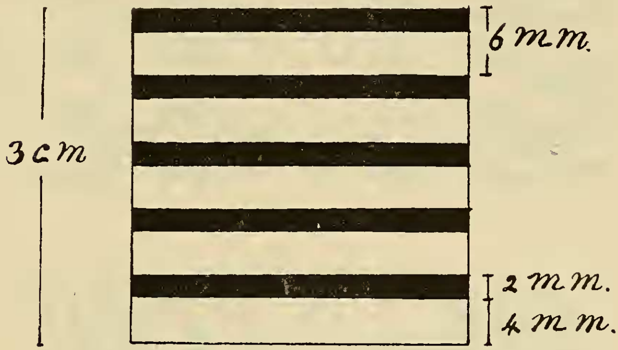
1. *Lighting.*—Experiments showed that the better the illumination the greater the distance at which the pattern was visible. A pattern which by day appears conspicuous, on account of the long distance at which it can be seen, at night may be difficult to see (*e. g.*, the Zebra).

2. *Contrast in Tone between the Components.*—The greater the contrast, the greater the blending distance of the pattern. A chequered pattern of black and white is visible at a greater distance than one composed of two shades of grey.

3. *Size of Components.*—The larger the components the greater the blending distance, all other factors remaining constant, as was shown in my previous paper (*loc. cit.*). If there be components of more than one size, then the smaller will blend first and the larger at a greater distance.

4. *Relative Size of the Components.*—For any given pattern there is a particular proportion of the components which gives the greatest blending distance.

Text-figure 6.



A specimen of the patterns used in Experiment No. 7.

EXPERIMENT No. 7.

Candles 1 ft. 6 ins. apart. Objects 2 ft. 2 ins. from candles.

Background grey. Objects square, 9 sq. cm. in size, divided horizontally into five black and white stripes of 6 mm. (see text-fig. 6).

						Pattern blends at
In No. 1	there is	2/8	black and	6/8	white	24 feet 2 inches.
" 2	"	3/8	"	5/8	"	25 "
" 3	"	4/8	"	4/8	"	26 " 11 "
" 4	"	5/8	"	3/8	"	26 " 9 "
" 5	"	6/8	"	2/8	"	25 " 9 "

A striped pattern is dealt with in the above summary; it shows that where the amount of black to white, or white to black, is very small, the blending distance is smaller than when there are about equal amounts of the two components.

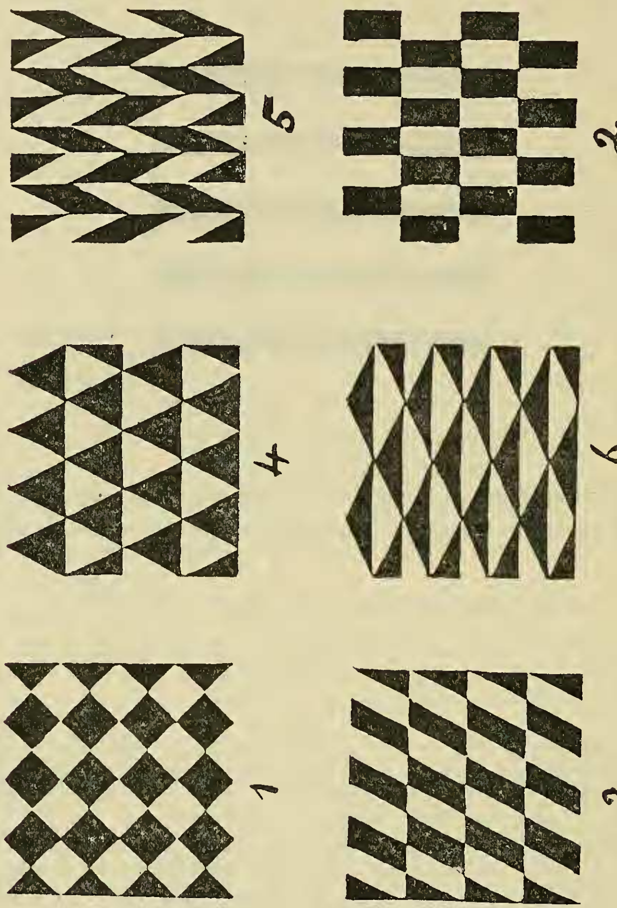
Referring also to experiment no. 9 (p. 397), it can be seen that for the types of patterns here dealt with there is similarly a particular proportion of black to white which gives the greatest blending distance under the experimental conditions.

5. *Shape of the Components.*—It has been shown that the visibility of plain objects depends upon the concentrations of their areas. Experiments show that, similarly, the blending distance of patterns is proportional to the concentration of the components of the patterns: the more concentrated the components, the greater is the blending distance, as is seen in the following experiment.

EXPERIMENT No. 8.

The blending distance of black and white patterns, of which the components are of the same size but of different shape. Experimental conditions: Candles 11 ins. apart, and 2 ft. from glass plate on which patterns were fixed.

Background behind glass plate, of grey paper, at such a distance that it is of the same tone as the patterns after they have blended. Text-fig. 7 shows the patterns used. The following table gives the length of the circumference of the component and the blending distance :—



Text-figure 7.

Patterns whose components are of the same size but of different shape. These were used in Experiment No. 8.

Pattern.	Length of circumference of component.	Blending distance.
No. 1	28·3 mm.	48 feet.
„ 2	30 „	47·5 „
„ 3	32·5 „	43 „
„ 4	32·5 „	43 „
„ 5	42·5 „	40 „
„ 6	42·5 „	40·5 „

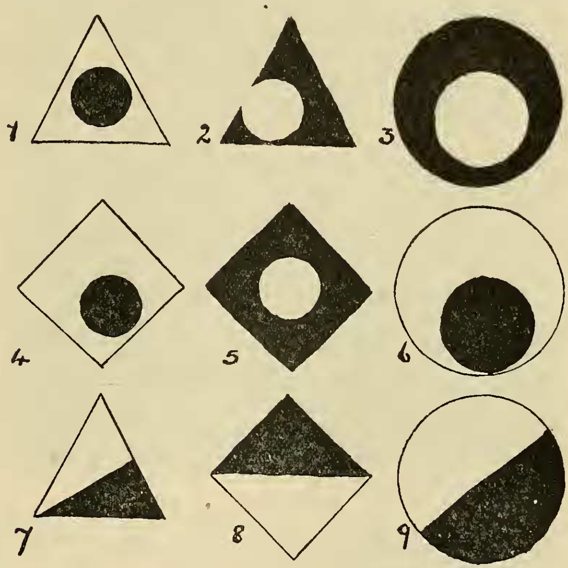
(Mean of six observations.)

The experiment shows that the smaller the circumference of the component, and therefore the greater its concentration, the greater the blending distance of the pattern.

With plain objects the circle is the most visible shape which they can have; so with patterns, the circle gives rise to the greatest blending distance.

Patterns composed of only two components require special consideration, as they have an important bearing on the subject of conspicuous patterns, as will appear later. It has been seen that the larger the pattern the greater the blending distance; it follows that, in order to give an object a pattern which will blend at the greatest distance, only two components must be used, thus making it as large as possible. To further increase the blending distance the relative tones of the two components must be as far removed as possible, and at least one of the components must have as concentrated an area as possible.

Text-figure 8.



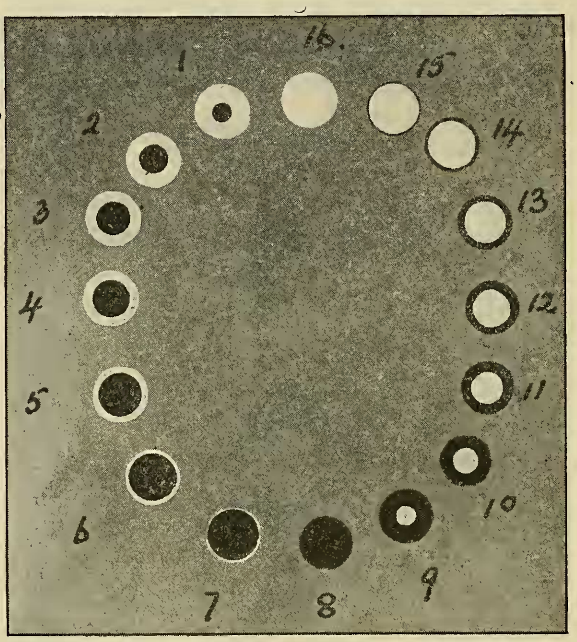
1–6. Patterns in which one component has the most concentrated shape, namely a circle, and is surrounded by the other component. 7–9. Patterns in which neither component has the most concentrated shape.

If the object be a triangle, a square, or a circle, then these conditions would be fulfilled in figs. *1–6* of text-fig. 8. These patterns would blend at a greater distance than would those shown in figs. *7–9*.

It has been seen that a third factor affects the blending distance, namely, the relative proportion of the components.

If a series of circular objects be made, as in text-fig. 9, and be examined against a number of differently-toned backgrounds, it will be found that the blending distances are not the same for different backgrounds. If, for instance, they be examined against a white background, then in the case of nos. *1–7* no pattern-blending occurs: the objects appear as black spots. If, instead, the background be light grey, then the white blends

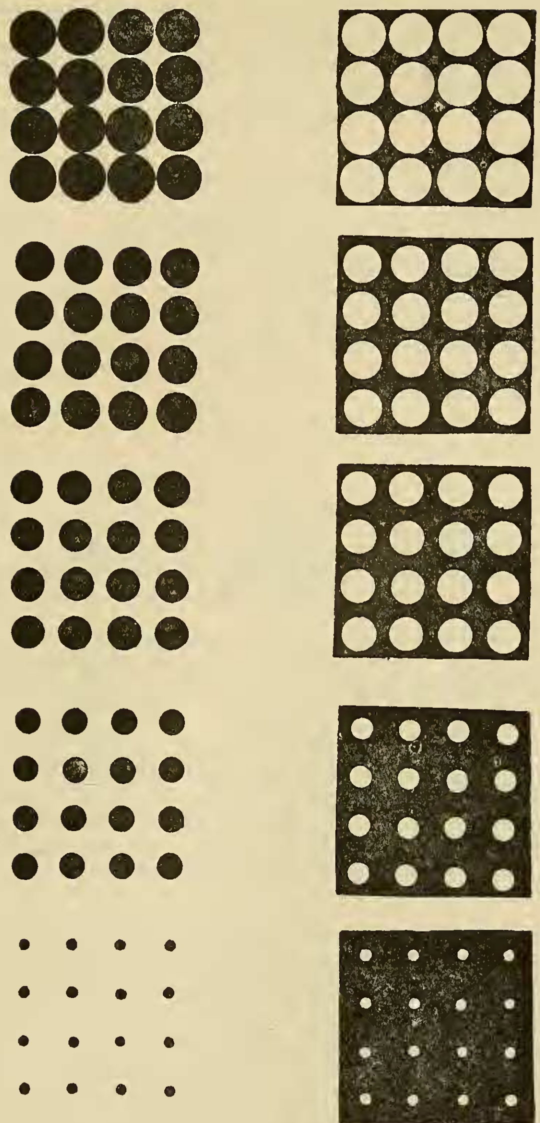
Text-figure 9.



A series of eye-spot patterns used in the experiment described on p. 401, and set out in Table I. The uppermost disc is white, the lowest black. The others contain from above down $\frac{7}{8}$, $\frac{6}{8}$, $\frac{5}{8}$, $\frac{4}{8}$, $\frac{3}{8}$, $\frac{2}{8}$, and $\frac{1}{8}$th of white, either concentrated in the centre, or in a ring round the periphery.

with the background and leaves the central black area visible after the white has ceased to be distinguishable from the background. This difficulty can be overcome by joining up a number of two-component patterns, and then finding the blending distance; this has been done in the following experiment.

Text-figure 10.



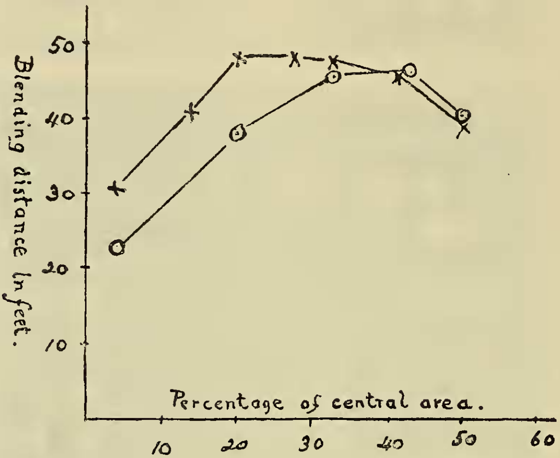
Portion of a series of spotted patterns used in Experiment No. 9.

Experiment No. 9.

The blending distance of black and white spotted patterns, as shown in above figure. The percentage of white to black varied from 10 to 60 per cent. Experimental conditions: Candles 1 ft. 6 ins. apart and 2 ft. 6 ins. distant from the pattern, which was placed on a glass plate with a grey background behind, as in experiment no. 8.

The following diagram (text-fig. 11) shows the blending distance in feet, plotted against the percentage of the spots to the whole pattern; the X shows the white-spot pattern, and the O the black centre. It can be seen that the white spot shows the greatest blending distance, which occurs when the white is approximately 20 per cent. of the whole.

Text-figure 11



Ordinates=blending distance of the patterns in feet. Abscissæ=percentage of the central components of the pattern. ⊙=the readings obtained when a black centre pattern was used (text-fig. 10, upper series). X=when a white centre pattern was used (text-fig. 10, lower series).

It can be seen that the greatest blending distance is produced by a white-centre pattern containing 20 per cent. of white, and it is shown also that the white-centre pattern blends at a greater distance than the black centre. It appears, therefore, that the blending distance of patterns is affected in the following ways:—

(1) By contrast in tone between the components: the greater the contrast, the greater the blending distance.
(2) By size of components: the larger the size, the greater the blending distance.
(3) By shape of components: the more concentrated the area of the components, the greater the blending distance.

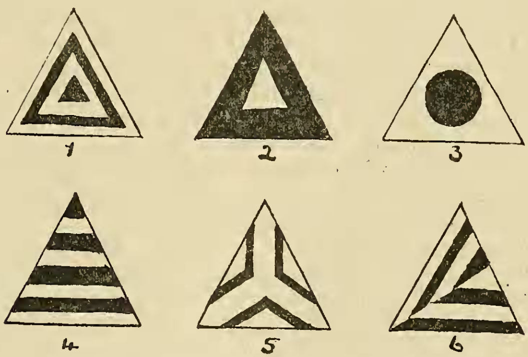
In order, therefore, to cover an object with a pattern which will blend at the greatest distance: (1) make the tone of the components a great contrast, black and white; (2) make the size of the components as large as possible, by reducing their number to two; (3) make the shape of the components as concentrated as possible, by making one of them a circle.

The consideration of the visibility of patterned objects against plain backgrounds can now be resumed. As before mentioned, a patterned object is visible as long as its pattern is visible; it follows that objects whose patterns blend at a great distance are more conspicuous than those whose patterns blend at a short distance.

There remains to be considered patterned objects which are visible against plain backgrounds after the pattern has blended at distance.

In a previous paper it was shown that, as regards visibility (as measured by the greatest distance at which the object is visible), patterned objects against plain backgrounds are neither more nor less visible than plain ones. It was also shown that, where the pattern interrupts the margin, the outline of the object appears blurred and difficult to define after the pattern has blended at

Text-figure 12.



1–3. Patterns which do not interrupt the margins of the object. 4–6. Patterns which interrupt two sides, three sides, and one side of the object.

distance. It follows that a further condition must be fulfilled in order that a patterned object may be as conspicuous as possible against a plain background: the pattern must present an uninterrupted margin, for example, as shown in text-fig. 12, *1–3*. If these patterns be viewed from beyond their blending distance, they will appear more defined than nos. *4*, *5*, and *6*, in which the pattern interrupts the margin. Apart from this, the visibility of patterned objects beyond the blending distance and against plain backgrounds is similar to that of plain objects against plain backgrounds. A patterned object can be made more conspicuous against a series of plain backgrounds than can a plain object, because, though a plain object can be made very visible against a single plain background by a strong contrast in tone with the background, nevertheless, when a series of backgrounds are used, then the object will appear inconspicuous against those similar in tone. On the other hand, with a patterned object, when the background is similar in tone to one of the components, then the other will make a strong contrast and cause the object to be easily visible.

It has been seen that the greatest blending distance which a pattern can have is one in which the white or lighter component is concentrated in the form of a circle, and that an object is most conspicuous against a wide series of backgrounds when it presents a pattern of only two components. Experiments were therefore made to discover which of two component patterns, the light-centre one or the dark, is the more conspicuous against a wide series of backgrounds. A series of discs were made, as shown in text-fig. 9, and examined against a series of backgrounds in the following manner:—

Text-fig. 1, B (p. 385) gives a ground-plan of the experimental conditions; it can be seen that the backgrounds are illuminated separately from the discs, which are fixed to a glass plate. By moving the backgrounds towards or away from the light, a continuous and wide range of tone in the background can be obtained. First, the background of white paper was moved so as to exactly match in tone that of the white in the discs. Under these conditions the all-white disc was invisible; of the rest, the disc with a white centre, 7/8 of the whole, was found to be the least visible, and next the disc with 6/8 white centre. The most visible disc was the all black.

The discs were examined in a similar manner over a wide series, and in each case the three least visible discs and the most visible were noted; the following table gives the results.

It can be seen that, except against backgrounds lighter than the white in the discs, the black-centre eye-spots are less visible than the white, and the appearances of the discs as seen from a distance show that the white-centre discs are the more visible.

The greater visibility of the white-centre eye-spots is especially marked when the backgrounds approach the dark end of the series; and as, as already shown, the backgrounds in Nature are, for the most part, of dark tone, it follows that white-centre eye-spot patterns of two components must be more conspicuous than black-centre patterns. Similarly, the white-centre pattern must be more visible than any other combination of black and white, because in this pattern the white is most concentrated, and therefore has the greatest visibility and the longest blending distance. It follows that against a series of plain backgrounds, and especially a series of relatively dark tone, the white-centre eye-spot pattern is the most visible one that an object can have.

TABLE I.

Backgrounds.	The three least visible discs.	The most visible disc.
White paper 1 ft. 3 ins. behind the discs gives a background considerably lighter than white of discs.	White, 7/8 white, 6/8 white.	Black disc.
White paper 1 ft. 3 ins. behind the discs gives a background lighter than white of discs.	White, 7/8 white, 6/8 white.	Black disc.
White paper 2 ft. behind the discs gives a background of the same tone as the white of the discs.	White, 7/8 white, 6/8 white.	Black.
White paper at 2 ft. 3 ins. gives a background a little darker than white of discs.	1/8 black, 7/8 white, white.	1/8 white.
White paper at 2 ft. 6 ins. behind the discs	1/8 black, 2/8 black, 5/8 white.	2/8 white.
White paper at 2 ft. 9 ins.	2/8 black, 3/8 black, 4/8 white.	1/8 white.
White paper at 3 ft. gives a background against which black and white are equally visible.	4/8 black, 5/8 black, 2/8 white.	Black and white discs.
White paper at 3 ft. 6 ins., or a grey paper at 1 ft. 11 ins., giving the same-toned background.	5/8 black, 4/8 black, 2/8 white.	7/8 white.
Grey paper at 2 ft. 6 ins.	5/8 black, 4/8 black, 1/8 white.	7/8 white.
Grey paper at 3 ft. 6 ins.	6/8 black, 7/8 black, 2/8 white.	6/8 white.
Grey paper at 5 ft.	7/8 black, black, 6/8 black.	7/8 white.
Grey paper at 5 ft. 6 ins. gives a background of the same tone as black of discs.	Black, 7/8 black, 6/8 black.	White disc.
Grey paper at 6 ft. 6 ins. gives a background darker in tone than the black of the discs.	Black, 7/8 black, 6/8 black.	White disc.

The most conspicuous pattern that an object can have against a series of plain backgrounds may now be defined :—

(1) The pattern must consist of two components.
(2) The components must differ widely in tone (black and white).
(3) The lighter component (white) must be concentrated at the centre in the form of a circle.
(4) The darker component must surround the white so that nowhere is there an interrupted margin.
(5) If the series of backgrounds be of low tone (as they are in Nature) then there must be more white than black in the pattern.

(C) *Plain Objects against Patterned Backgrounds.*

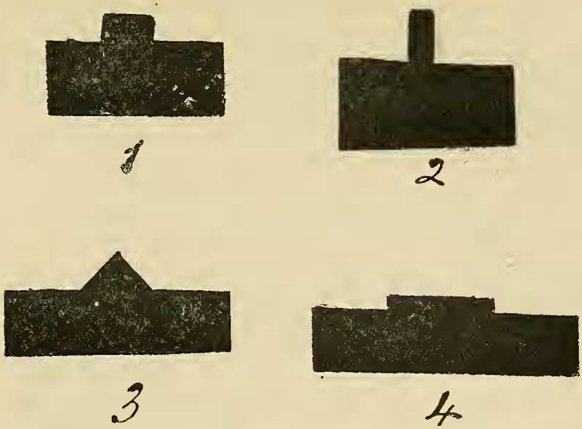
(1) If the object is visible after the pattern has blended at distance, then the factors which control its visibility are the same as those of plain objects against plain backgrounds. The outline of the object will, however, appear blurred just as when a patterned object, whose pattern is interrupted at the margin, appears blurred when viewed against a plain background. The conclusions are similar, the only difference being, that in one case the object is plain and the background patterned, whereas in the other the object is patterned and the background plain.

(2) If the object becomes invisible before the pattern of the background blends at distance, then the object may be seen against one component of the background ; in which case the factors controlling visibility will be similar as are those of plain objects against plain backgrounds, except that the near presence of an area of different tone will affect the visibility of the object. A black square on the white component of a checkered background will be less visible than on a plain white background (see experiments, nos. 2 & 3). With this exception, the factors controlling visibility are similar to those of a plain object against a plain background. The object may be visible against two or more components of the background. If the object is of the same tone as one of the background components, then the object will appear as a projection from the margin of one component.

Experiments were carried out to discover whether the factors controlling visibility were different from those of a black object against a white background, and it was found that, except for the decrease in visibility due to the presence of an area of black (in this case touching the object), the visibility was similar to that of a plain object on a plain background, except that the effect of shape of the object was rather different from its effect when dealing with plain objects against plain backgrounds, as seen in the following experiment *.

* This consideration has an important bearing on concealment by indented or scalloped margins; a series of experiments has been carried out from this point of view which, however, are only of present interest in so far as they show that an even margin is a factor for conspicuousness.

Text-figure 13



Objects of the same size but of different shape lying at the junction of a black and white background as used in Experiment No. 10.

Experiment No. 10.

The visibility of black objects projecting from the margin of a large black mass.
The objects are all of the same size but of different shape, as shown in the text-figure.
Experimental conditions: Candles 1 ft. 3 ins. apart and 3 ft. 6 ins. from objects.

Object	no.	1	visible at	57	feet.
,,	,,	2	,,	54	,,
,,	,,	3	,,	49·5	,,
,,	,,	4	,,	32	,,

Compare with Experiment No. 5.

The object may be visible against two or more components of a patterned background, and may be different in tone from either component.

Text-figure 14.

1. A grey disc placed over the junction of a black and white background. If the disc approaches in tone more nearly the white of the background than the black then from a distance it will be seen as in no. 2; if more nearly the black, then as in no. 3.

If a grey disc be placed over a black and white junction, as in text-fig. 14, and be viewed from gradually increasing distances, a point will be reached at which one half of the disc is blended with one component of the background, whilst the other half is seen as projecting into the other component. If the grey disc more nearly approaches the black in tone than the white, then at a distance it will appear as in text-fig. 14, *3*; if it more nearly approach the white, then as no. *2*.

The following experiment illustrates this appearance :—

Experiment No. 11.

Candles 1 ft. apart and 2 ft. distant from background.
Background half black and half white (7 × 5 ins.).

Objects circular, 20·4 sq. mm., eight in number and ranging in tone from black to white. Objects placed exactly over the junction of the black and white of the background.

	Visibility distance.	
1. Black	33 feet.	Visible as a dark projection into the white of the background.
2. „	30 „ 5 inches.	
3. Dark grey......	37 „ 5 „	
4. „ „	20 „	
5. „ „	18 „ 5 „	Visible as a light projection into the black of the background.
6. Light grey ...	23 „ 5 „	
7. „ „ ...	34 „ 7 „	
8. White	35 „ 9 „	

An object was prepared of such a grey tone that it was neither seen as a white nor as a black projection into the background's components. This object was the least visible disc and visible at 16 ft. 4 ins.

Some similar experiments were carried out with backgrounds composed of different tones of grey instead of black and white, and it was found that the objects likewise appeared as projectors into one or other of the components, according as to whether the object more nearly approached in tone one or other of the components.

If, for instance, the background was made of two dark grey tones, then only the darkest objects appeared as black projectors against the lighter of the two components.

As in Nature backgrounds are dark in tone rather than light, it follows that light grey or white discs will be more visible under these conditions, *i. e.*, when seen against two or more components of a patterned background, than dark discs.

As mentioned in the last experiment, there is one tone of grey against which black and white are equally visible, and when the object is of this particular tone it never appears as a projective from one component on to the other. Against backgrounds composed of tones other than black and white, there is similarly one grey tone which the object may have which will cause it to give a similar appearance.

An experiment was carried out with discs of this tone to discover whether the effect of size of the object was similar or not to that found when dealing with plain objects against plain backgrounds. As seen in the following experiment, the effect is similar :—

EXPERIMENT No. 12.

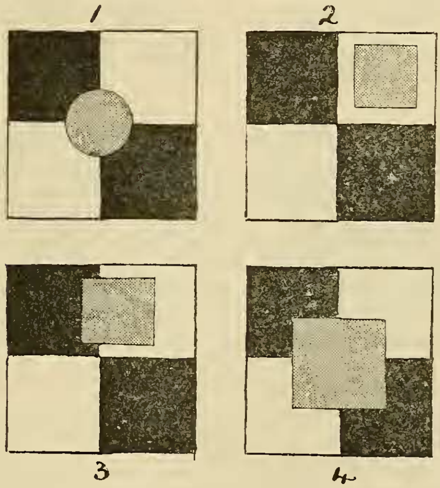
Candles 1 ft. apart and distant 2 ft. from background.
Background as in Experiment No. 11.

Objects of various sizes were made of grey discs of such a tone that they were seen neither as black nor as white projections into the components of the background. These objects were placed over the junction of the black and white components of the background. The following table gives the visibility of the discs:—

Size of grey disc.	Distance at which visible.
41·9 sq. mm.	27 feet 5 inches.
30·2 „	24 „ 2 „
20·4 „	19 „ 5 „
6·1 „	9 „ 1 „

The effect of shape was found to be different, as in the case of objects of the same tone as one of the components of the background. (See experiment no. 10.)

Text-figure 15.



Objects placed on more than two components.

A few observations were made with objects placed in front of more than two components, as in text-fig. 15, *1* & *4*, but no special difference was noted from those when only two components were covered by the object.

Another arrangement of an object against a patterned background remains to be mentioned. The object may more or less resemble, both in tone, in shape, and in position, one of the components of the background; in this case, though it may appear to be invisible on account of this similarity and thus to come under a separate category, nevertheless this is not so, as it will fall naturally under one of the conditions already considered. For instance, a very light grey object may resemble the light square of the checkered background, both in shape, size, and position, as in text-fig. 15, *2*; but it can also be considered under the heading "Objects falling on one component of the background." If it falls as in text-fig. 15, *3*, then on two components of background; if as in no. *4*, then as an object visible after the pattern has blended at distance.

It appears, therefore, that a direct resemblance does not necessitate a separate consideration.

Conclusions.—The factors which make for the conspicuousness of plain objects against patterned backgrounds appear to be similar to those when plain backgrounds are used. If the pattern of the background interrupts the object's margin, then outline blurring occurs. The near presence, or contact with the object, of an area of tone similar to the object makes it less visible.

(D) *Patterned Objects against Patterned Backgrounds.*

If a patterned object be viewed against a patterned background from gradually increasing distances, several different appearances may be seen.

(1) The pattern of the object may blend before the pattern of the background, in which case it will appear as a plain object against a patterned background.

(2) The pattern of the background may blend before the pattern of the object. The object will then appear as a patterned one against a plain background.

(3) The patterns of object and background may both blend and yet the object may still be visible against the background, in which case the object will appear plain against a plain background.

These three conditions have already been dealt with.

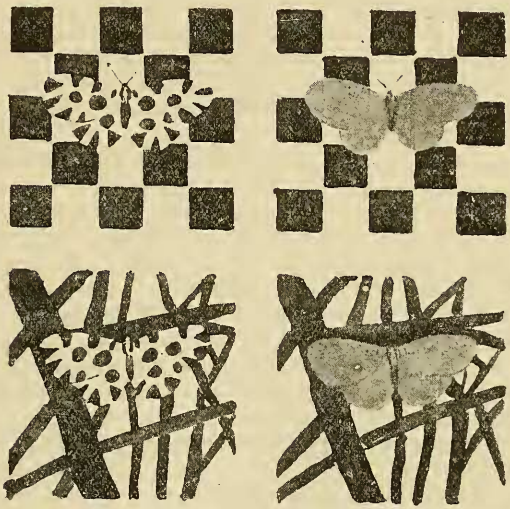
(4) A fourth appearance may occur. The object may not be visible, although neither its pattern nor the pattern of the background have blended.

Before dealing with this appearance the first three must be briefly considered. It has already been shown in my previous paper (*loc. cit.*) that though a patterned object is not less visible than a plain one, nevertheless, if the pattern interrupts the margin, then its outline after pattern-blending appears blurred and indistinct, as compared with a plain object of the same tone as the patterned one after blending.

It has also been mentioned (p. 402) that outline blurring similarly occurs when the object is plain and the background patterned. It might therefore be concluded that against patterned backgrounds the outline of a plain object would appear just as blurred as that of a patterned one beyond the blending distance of the background's pattern; but when both the object's pattern and the background's pattern are blended, and provided that both interrupt the junction of object and background, then the blurring effect of these two interruptions are added, and cause the junction of object and background to appear much more indistinct than when only one pattern interrupts.

In text-fig. 16, if in each case the insects remain visible after the patterns are blended, then the outline of the patterned one will be the more indistinct when the tone of the patterned insect after pattern-blending is the same as that of the plain insect.

Text-figure 16.



Visibility of insects on different backgrounds.

It follows that animals with a pattern which interrupts the margin will be less visible than plain animals against a patterned background as well as against a plain one; and further, that against a patterned background an uninterrupted margin will be as necessary for conspicuousness as against plain backgrounds; in fact, experiments appeared to show that it was more necessary, because the blurring effect of the background pattern required to be counteracted.

In Nature, a pattern which interrupts the margin must be a great aid to concealment against patterned backgrounds, because the backgrounds are irregular and the animal must often be seen with one or more of its margins against a single component of the background, as shown in text-fig. 16.

The conclusions as regards conspicuousness which have already been made must thus apply to patterned objects against patterned backgrounds. There remains to be examined only the fourth condition, in which the object cannot be seen though both the object's and the background's patterns remain visible. This invisibility is due to a great similarity between the patterns of object and background in size, shape, and relative tone of the components. It is obvious that the most conspicuous pattern will be inconspicuous against a background made of a similar, or closely similar, pattern. For this reason, under these special conditions, it is not possible to define a pattern which will be especially conspicuous, unless the pattern of the background is also defined.

It may be concluded, therefore, that the pattern which has been called the white centre eye-spot pattern is a most conspicuous one against every background with the exception of backgrounds themselves composed of eye-spot patterns. It follows that in Nature the white eye-spot pattern must be very conspicuous, provided that this type of pattern is not continuously found as a background.

White centre eye-spot patterns in Nature.—Natural backgrounds were examined in order to discover whether this type of pattern was to be found and to what extent, and it was at once noticed that they were very uncommon; a morning's foray amongst woods, fields, hedgerows, and broken country resulted in only a few examples. It is not difficult to make such patterns artificially out of doors; for instance, by laying round white stones on circular patches of dark moss, by placing shining leaves over dark rough ones, by viewing pierced leaves against the light, and in many other ways. Natural eye-spot patterns may be conveniently described under the following headings:—

1. *On bare ground.*—(*a*) Due to irregularities of the surface. Working with plasticene the pattern can be produced by a shallow conical pit with a flat bottom, by a truncated cone lying on its base, or by a cylinder standing in the middle of a cylindrical depression; in each case top lighting is necessary. Viewed from above, a light centre dark-margin circular pattern is seen; the pattern does not perfectly reproduce the one desired, because the centre instead of being lighter in tone than the background is either of the same tone or somewhat darker. It is evident that by artificial methods this pattern can only be reproduced with difficulty, and thus its occurrence in Nature must be very rare. By prolonged search isolated examples are to be seen.

(*b*) Due to the surface being of broken tones; a light stone or one reflecting the light from the sky when lying on a circular dark patch will give rise to the pattern. Examples of this nature are not difficult to find, but they are never numerous and always isolated.

2. *On grass and other short vegetation.*—Except for flowers, which are considered elsewhere, the eye-spot pattern is very rarely seen; occasionally light reflected from a shiny leaf supplies an example.

3. *Rank vegetation.*—Light from a shiny leaf, or a leaf in strong light against shadow, occasionally forms the pattern.

4. *Scrub, hedgerows, and wood margins.*—Circular leaves in very strong light against dark shadows often give rise to a pattern which is somewhat like a white centre eye-spot one, but distinction must be made between a pattern consisting of light spots on a dark background and the pattern under consideration. The first is common in Nature ; the second requires a light centre, a dull margin, and a background of a different tone. Occasionally this arrangement is to be seen among vegetation, but only isolated examples are to be found.

5. *Light woods.* — Here are sometimes to be seen patterns similar to those described under the previous heading. Where sunlight penetrates through foliage and falls on dark ground or foliage beneath, white spots of light result, and when these happen to fall on dark objects they produce the white centre eye-spot pattern. According to the frequency with which they happen to fall on dark objects is the prevalence of the pattern. When the ground beneath the trees is much broken in tone, several may be seen from a single station. Several conditions are, however, necessary for their production—an uncovered more or less vertical sun, a not completely dense canopy of foliage, and a broken ground beneath.

6. *Heavy woods.*—If the foliage be not too dense the pattern may be produced as described in no. 5.

7. *Sky.*—On looking up at the sky through foliage, white spots are to be seen in the intervals between the leaves and where there are holes in them. If a white spot happens to be surrounded by a dark shadow or a deep-toned leaf, then a white-centre dark-margin eye-spot results. A small number of these are always to be seen. It may be pointed out that though man is not accustomed to view foliage in this way, many animals of low stature and whose eyes are set looking upwards as well as forwards must frequently take this view.

8. *Water.*—Very small pools of water when they reflect the sky and when, as is often the case, they are surrounded by a ring of moist and therefore dark-toned ground, have the appearance of the eye-spot pattern. Foliage overhanging water or floating upon it also rarely gives rise to the same pattern, the sky reflected from the water forming the white centre and the foliage the dark ring. Drops of water and dew under some conditions of lighting give rise to an abundance of the pattern of a transitory nature.

9. *Flowers.*—By far the most common examples in Nature of the eye-spot pattern are to be found in flowers. A dark centre eye-spot is as common as a light centre. There can hardly be a doubt that flowers are purposely conspicuous ; it is therefore noteworthy that their patterns conform to the rules which experiments have decided must be followed in order that a pattern may be conspicuous in Nature.

Flowers are, as a rule, circular; their patterns consist of seldom more than two components, one being concentrated in the middle in the form of a circle, and there is usually a strong contrast in tone (and colour) between the two components.

It might be thought that these arrangements of pattern in flowers were due to convenience of growth; but the eccentric shapes and patterns assumed where special animals are sought for the purpose of fertilisation indicate that flowers are not forced by growth to assume the circular shape and eye-spot pattern.

In conclusion it may be said that, except in the case of flowers, white-centre dark-margin eye-spot patterns are rarely to be seen in Nature and are almost always isolated. Sunlight penetrating through foliage on to broken ground and sky views through foliage are the two most common causes. As regards flowers, eye-spot patterns are very common, but the centre is as often darker than the margin as *vice versa*.

It follows that animals presenting this type of pattern must be considered to be conspicuous in Nature.

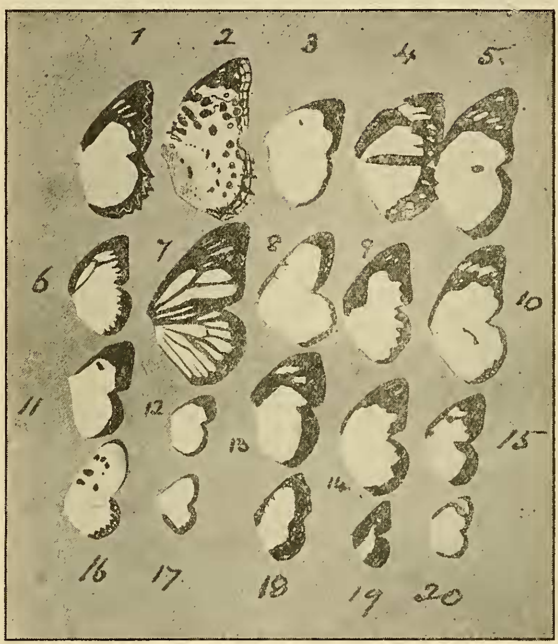
Part II.

Having by experimental methods defined the types of pattern which render an object conspicuous, attention was turned to the animal kingdom to discover whether examples of these types could be found and, if present, what was their distribution. Search was made among the Lepidoptera because their wings offer a plain, flat patterned surface, and thus the complicating factor of solidity is avoided. Rather than search through a large amount of material, it was decided to deal thoroughly with a definite amount, viz., the Indian Lepidoptera. Moore's 'Lepidoptera Indica' was the work chosen, because of its good coloured illustrations of each species. On glancing through these plates several types of pattern were found which previous consideration showed would render these insects conspicuous. The first type to be dealt with is shown in text-fig. 17. It can be seen that the pattern consists of a central white, or light yellow, area surrounded by a black margin, so that the four wings combined present an irregular, white-centred, black-margined pattern. The margin of the wings is, except in two cases (nos. *1* and *4*), not scalloped. The black marginal band is sometimes broken by small spots or bands of light tone, but only in the case of no. *2* is the margin interrupted by pattern.

This type of pattern presents, therefore, those characters which previous consideration has shown must render the insect conspicuous in Nature: the table on p. 412 gives its distribution among genera of the Indian Lepidoptera.

Salatura (text-fig. 17, *7*) and *Acidalia* (no. *2*) do not conform to the type in several respects. In *Salatura* the centre white area is broken up by dark bands, and in *Acidalia* by black spots, besides which there is a half-tone area at the centre of the wings. They are introduced for several reasons, as will appear later. Certain butterflies are presumed to be protected from the attack of enemies by ill-flavour; further, it has been noted that these insects are conspicuous in Nature (and it has been suggested that they are conspicuous in order to warn enemies); and lastly, it has been noted that the pattern and coloration of these insects are

Text-figure 17.



Types of all the genera illustrated in 'Lepidoptera Indica' which present patterns of the first type under consideration.

1. *Cethosia.* 2. *Acidalia.* 3. *Catopsilia.* 4. *Elymnias.* 5. *Apatura.* 6. *Appias & Huphina.* 7. *Salatura.* 8. *Pareba.* 9. *Catophaga.* 10. *Limnas.* 11. *Eurymus.* 12. *Kibreeta, Nirmula, & Terias.* 13. *Ixias.* 14. *Hyposcritia.* 15. *Anaphæis.* 16. *Telchinia.* 17. *Chrysophanus.* 18. *Stiboges.* 19. *Daimio.* 20. *Callosune.*

mimicked by insects which are not thus protected by ill-flavour, in order that they may gain protection by means of a false cloak. The pros and cons of this contention cannot be discussed here, but it is remarkable that many of the insects presenting the type of pattern under consideration belong to what are considered to be protected genera, or to what are considered to be

TABLE II.

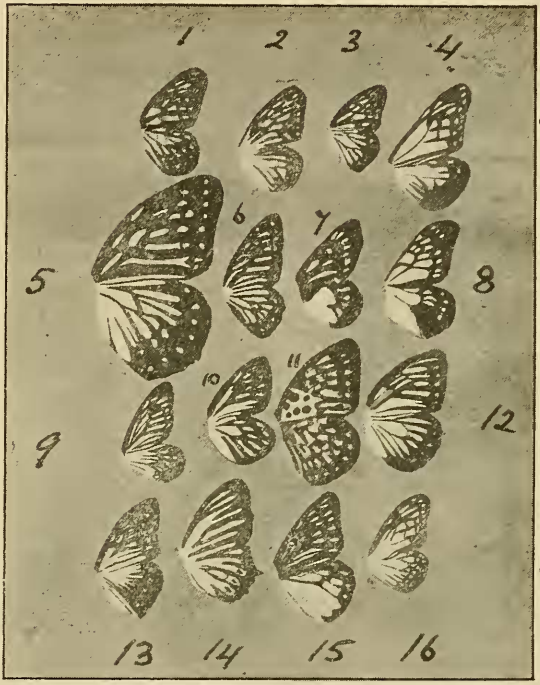
Family.	Subfamily.	Genus.	Male.	Female.	Both sexes.	Protected.	Mimicry.	Neither protected nor mimicry.
Nymphalidæ.	Euplœinæ.	*Limnas*	...	...	×	×		
		Salatura	...	...	×	×		
	Elymniinæ.	*Elymnias*	...	×	...	...	×	
	Nymphalinæ.	*Apatura*	...	×	...	...	×	
	Argynninæ.	*Cethosia*	...	..	×	×		
		Acidalia	...	×	...	...	×	
	Acræinæ.	*Pareba*	...	...	×	×		
		Telchinia	...	...	×	×		
Riodinidæ.	Nemeobiinæ.	*Stiboges*	...	...	×	...	...	×
Pieridæ.	Pierinæ.	*Anaphæis*	...	...	×	...	...	×
		Appias	...	...	×	...	...	×
		Huphina	...	...	×	...	...	×
		Hyposcritia	...	...	×	...	...	×
		Catophaga	...	...	×	...	...	×
	Coliinæ.	*Kibreeta*	...	...	×	...	...	×
		Nirmula	...	...	×	...	...	×
		Terias	...	...	×	...	..	×
		Catopsilia	...	...	×	...	...	×
		Ixias	...	...	×	...	...	×
		Callosune	...	...	×	...	...	×
		Eurymus	×	...	...	...	...	×
Lycænidæ.	Lycænopsinæ.	*Castalius*	...	...	×	...	...	×
	Chrysophaninæ.	*Chrysophanus* ...	×	...	...	...	...	×
Hesperiidæ.	Celænorrhinæ.	*Daimio*	...	...	×	...	...	×
5	11	24	2	3	19	5	3	16

unprotected insects mimicking protected. It can be seen that out of 24 genera forming Table II., 5 are described by Moore as protected and 3 as exhibiting mimicry; whereas out of all the 600 genera described only 41 are mentioned as either protected or mimicking. No reason can be given why the other 16 genera (for the most part belonging to the Pieridæ) present a conspicuous pattern *. It is, however, noteworthy that the sexes are alike, with the exception of *Eurymus* and *Chrysophanus*, where the pattern is confined to the male. Several of the genera are amongst the commonest of butterflies, and at certain times collect

* The Pierinæ and Coliinæ are considered by some observers to be "protected" insects.

together and migrate in immense swarms. *Salatura* was introduced into this table because it shows a considerable resemblance to the next type to be considered. The bands of dark tone crowning the central light area have been drawn too boldly and of too dark a tone, which makes the resemblance closer than it really is.

Text-figure 18.



Types of all the genera illustrated in 'Lepidoptera Indica' which present patterns of the second type under consideration.

1. *Parhestina.* 2. *Parantica.* 3. *Orinoma.* 4. *Caduga.* 5. *Penthema.* 6. *Paranticopsis.* 7. *Delias.* 8. *Calinaga.* 9. *Cadugoides.* 10. *Caduga.* 11. *Neurosigma.* 12. *Metaporia.* 13. *Hestina.* 14. *Radena.* 15. *Prioneris.* 16. *Bahora.*

Examples of the second type of pattern which must render the insect conspicuous in Nature are shown in text-fig. 18. It can be seen that the insects present an uninterrupted margin, the pattern nowhere reaching the margin, and that at the margins there is an area of dark tone, whilst the centre of the wings is much lighter in tone. As before, there is no scalloping or irregularity of the margin. It follows that this pattern conforms to the factors which have been considered to make for conspicuousness. Table III. shows the distribution of this second type of pattern. At a short distance the central patterned area will become blended and give rise to a light grey tone, and the insect then has an appearance similar to the type first considered. As before, it can be seen that out of 18 genera, 7 are protected and 7 mimic: in this case, therefore, the conspicuous pattern is accounted for in the case of 14 out of the 18 genera; 4 remain unaccounted for. It is noteworthy that in all cases the sexes are alike.

Table III.

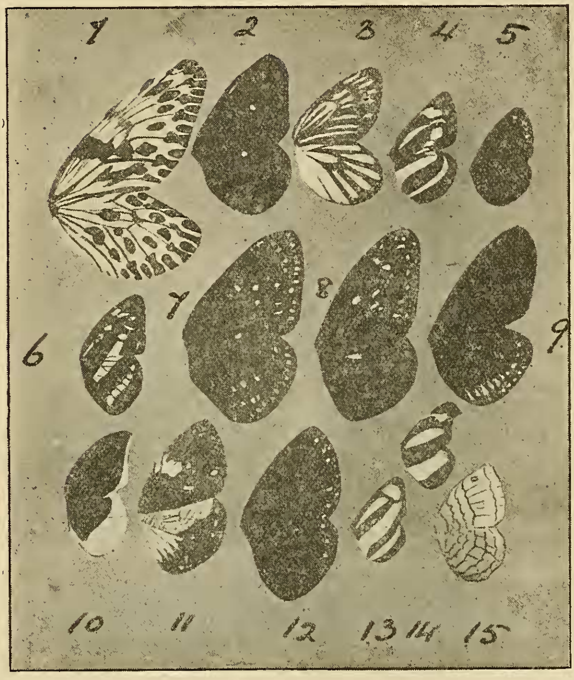
Family.	Subfamily.	Genus.	Male.	Female.	Both sexes.	Protected.	Mimicry.	Neither protected nor mimicry.
Nymphalidæ.	Euplœinæ.	*Radena*	...	...	×	×		
		Tirumala	...	...	×	×		
		Bahora	...	...	×	×		
		Parantica	...	...	×	×		
		Caduga	...	...	×	×		
	Satyrinæ.	*Orinoma*	...	...	×	...	...	×
	Elymniinæ.	*Melynias*	...	...	×	...	×	
	Nymphalinæ.	*Hestina*	...	...	×	...	×	
		Parhestina	...	...	×	...	×	
		Neurosigma	...	...	×	...	.	×
		Penthema	...	...	×	...	...	×
	Calinaginæ.	*Calinaga*	...	...	×	...	×	
Papilionidæ.	Papilioninæ.	*Cadugoides*	...	...	×	...	×	
		Paranticopsis ...	...	...	×	...	×	
Pieridæ.	Pierinæ.	*Metaporia*	...	...	×	×		
		Delias	...	...	×	×		
		Prioneris	...	...	×	...	×	
	Eroniinæ.	*Pareronia*	...	...	×	...	...	×
3	8	18	—	—	18	7	7	4

Conspicuous pattern combined with an absence of secondary sexual dimorphism is so frequently associated with a protected species, that attention must be drawn to the fact that some of the unaccounted-for genera in both tables may be protected genera, although not mentioned as such in the work consulted.

Finally, all the insects which are mentioned by Moore as being either protected by ill-flavour or mimicked by other species, are briefly considered in order to see whether or not they present patterns which experiments have shown must be conspicuous in Nature *.

Text-fig. 19 shows their patterns. No. *3* is like *Salatura*, a stage between the first and second types. There is, however, an absence of a defined dark margin to the hind wings, the margins are not scalloped, and the pattern does not interrupt the margin, though it approaches near to it; it thus presents some of the characters making for conspicuousness.

Text-figure 19.



Types of all the genera mentioned in 'Lepidoptera Indica' as being "protected" beyond those already given in text-figs. 17 & 18.

1. *Hestia*. 2. *Menama*. 3. *Piccarda*. 4. *Bimbisara*. 5. *Calliplœa*. 6. *Condochates* & *Neptis*. 7. *Euplœa* & *Pademna*. 8. *Stictoplœa*. 9. *Penoa* & *Crastia*. 10. *Cynitia*. 11. *Danisepa* (the dark tone of this insect should be darker). 12. *Isamia*. 13. *Stabrobates*. 14. *Libythea* (? protected). 15. *Ergolis*.

Nos. *2*, *5*, *7*, *8*, *9*, and *12* are conspicuous in so far as they present a large, dark, unpatterned area; their margins are not scalloped or interrupted by pattern; the marginal spots, when

* Mimicry within the Papilioninæ is only referred to once in an indefinite manner.

present, would, however, tend to mask the outline. As to whether or not these insects are conspicuous in Nature must depend upon the tone of the backgrounds against which they are commonly to be seen; if the backgrounds be light in tone they would be conspicuous insects, but if the insects lived in dark forests, for instance, they would not be especially conspicuous.

No. *11* is similar to the last except that both wings present a large white patch which must make the insect more conspicuous. The patch on the fore wing interrupts the anterior margin and must therefore have the opposite effect.

No. *10* presents a black-centre white-margin pattern which, as has been seen, is almost as conspicuous as the white-centre black-margin pattern.

Nos. *4*, *6*, *13*, & *14* present patterns which do not interrupt the margin but, instead, follow it; there are three central bands or rows of spots which are surrounded by black, and the margins of the wings are not scalloped, thus several factors making for conspicuousness are present.

In no. *1* the pattern everywhere interrupts the margin, and the margin of the wing is not scalloped. The pattern is not therefore a conspicuous one, the general tone of the insect is light and the wing-expanse large; thus, in spite of an inconspicuous pattern, the insect might be conspicuous if its natural environment were of dark tone—if, for instance, it were a forest insect. It may be noted that another species of the same genus (see text-fig. 20, *4*) presents a typical conspicuous pattern.

No. *15* presents no character making for conspicuousness; the margin is somewhat scalloped, the pattern interrupts the margins, the insect, as drawn, is coloured a middle brown with a darker line pattern, and is mimicked by *Rohana parisatis*. With the exception of this genus and *Hestia*, the patterns of these protected or mimicked insects all show one or more characters which make for conspicuousness, and present patterns much less perfectly conspicuous than the two types first dealt with. The first type conforms very closely to the pattern which experimental consideration indicates must be the most conspicuous. Even the larger proportion of black to white tone in the pattern conforms; as the backgrounds in Nature are for the most part dark rather than light in tone, so there should be a greater proportion of white to black in the pattern. It is not possible to show why less perfect types are to be found; perhaps they present a stage in the evolution of the conspicuous patterns, or that for some reason a more perfect pattern is not required by these insects. On referring to text-figs. 17 and 18 it can be seen that the mimicking species present patterns which are not so perfect as the models. *Acidalia*, for instance, could with justice be removed from the first series.

As a contrast to these patterns four inconspicuous patterns are shown in text-fig. 20, *1*, *2*, *3*, *5*; it can be seen that in three the margin is scalloped; in nos. *1* and *3* the pattern interrupts the anterior and lateral margins; in no. *5* it interrupts the anterior margin. In no. *2* the pattern of eye-spots and irregular bands is confined to the outer margins of the wings, whereas the rest of the wings is of an even dull tone (brown); in nos. *1*, *3*, and *5* the pattern is likewise more or less confined to the margins, leaving the centre of the wings plain; in no. *1* the outer margin is fringed by outstanding scales which cause the margin to appear indistinct. Unprotected butterflies show, as a rule, one or other of these and other characters which cause their outlines to blend into their surroundings, the pattern is confined to the wing margins and it interrupts the margin, and the margin is

Text-figure 20.

Insects with inconspicuous patterns.

1. *Pontia daplidice* ♀. 2. *Anadebis himachala* ♂. 3. *Lethe neelgheriensis* ♀. 4. *Hestia hadenii* ♀. 5. *Pazala sikkima* ♀. 6. *Hestia malabarica* ♀.

scalloped. On the other hand, those insects which have been considered to present conspicuous patterns show none of these characters: their outlines are not scalloped, their patterns are not especially confined to the margin and do not interrupt the margin.

Finally, it may be said that whilst the inconspicuous pattern of insects conceals their outline, the silhouette of an insect against its surroundings (the patterns may or may not mimic the backgrounds), the conspicuous pattern accentuates the margin.

Concluding Remarks.

Many experiments and observations have shown that the patterns and coloration of animals are related to their environment: such terms as Protective Resemblance, Obliterative Shading, etc., indicate the lines of research along which knowledge has been acquired, and which is conveniently condensed in the following table by Prof. Poulton. The basis of this classification is a resemblance, or otherwise, of the animal's coloration to its natural background. Further differentiation is achieved

Table IV.

A. Apatetic colours = colours resembling some part of environment.
- (1) Cryptic (*a*) procryptic = protective resemblance.
  - (*b*) anticryptic = aggressive resemblance.
- (2) Pseudo-sematic = false signalling.
  - (*a*) pseudo-sematic = protective mimicry.
  - (*b*) pseudo-episematic = aggressive mimicry or alluring.

B. Sematic colours = signalling colours.
- (1) Aposematic = warning.
- (2) Episematic = recognition marks.

by division according to the utility or function which this resemblance, or the reverse, has. These functions have to do with the escape from enemies, the procuring of food, and recognition by members of the same and other species. It follows that the patterns of animals must be closely related to the visual perception of their enemies, their prey, and their friends. A classification from this point of view would seem, therefore, to be the most natural, and the following table was therefore prepared.

Table V.

<table>
<tr><td rowspan="7">Colour and Pattern.</td><td>Unrelated to the visual perception of other animals:</td><td colspan="3">for the absorption of Light Rays:
for the absorption of Heat Rays:
Excretory products etc.</td></tr>
<tr><td rowspan="6">Related to the visual perception of other animals.</td><td rowspan="3">Inconspicuous to other animals:</td><td>to the eyes of enemies</td><td>= protective coloration.</td></tr>
<tr><td>to the eyes of prey</td><td>= aggressive coloration.</td></tr>
<tr><td>to the eyes of friends</td><td>= ?</td></tr>
<tr><td rowspan="3">Conspicuous to other animals:</td><td>to the eyes of enemies</td><td>= attracting and repelling, and warning coloration.</td></tr>
<tr><td>to the eyes of prey</td><td>= to allure prey as in Mantidæ.</td></tr>
<tr><td>to the eyes of friends</td><td>= social signals, sexual signals.</td></tr>
</table>

If the consideration of pattern from this aspect be of value, then an experimental analysis carried out with artificial patterns and the human eye must be a sound foundation for the study of the subject, at any rate, as regards the visual perception of mammals, provided the human eye is not widely different from that of mammals as a whole. The results of this line of investigation show that patterns of animals will bear such an intense study, and indicate that many details of pattern may be of value although they have, up to the present, and on negative evidence, been considered to be unrelated to the visual perception of their own and other species.

In view of the fact that sight is a most valuable organ of perception, and therefore a most powerful weapon in the struggle for existence, it follows that a study of pattern from this point of view is likely to throw light on some of the important problems of Nature.